THE COMPARATIVE ANATOMY AND PHYLOGENY OF THE BETULACEAE

BY

JOHN WALTON HALL

B.S., University of Massachusetts, 1940
M.S., University of Massachusetts, 1942

AN ABSTRACT OF A THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN BOTANY
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THE COMPARATIVE ANATOMY AND PHYLOGENY OF THE BETULACEAE

The anatomical method is playing an ever increasing role in the attempt by botanists to arrive at a natural system of classification of the plant kingdom. A series of anatomical dicta has been developed by wood anatomists within the last few decades, upon which phylogenetic interpretations are based. Then, data from paleobotany, floral and inflorescence anatomy, nodal anatomy, pollen morphology, floral morphology, cytology, gametophyte development, etc., are harmonized and correlated with the data derived from wood anatomy. Thus, evidence from all fields of plant study are employed in formulating conclusions on the phylogenetic position of the group of plants in question.

The Betulaceae — the subject of the present investigation — are members of a group of plants, the "Amentiferae", whose phyletic position has long been debated. It was for this reason that the family was chosen for further research. A comparative study of the secondary xylem of the family was made in order to determine the degree of specialization among the genera of the family and of the family as a whole. As a by-product, descriptions of the woods of the genera and of the family were prepared.

Prepared slides of 73 species in the six genera of the family (Alnus, Betula, Corylus, Ostryopsis, Carpinus and Ostrya) were studied. The results of this anatomical investigation are briefly summarized below.

1. All the Betulaceae are diffuse-porous, and have angular, thin-walled, very small, very numerous vessels arranged in pore clusters, pore multiples and solitary pores. The fibers are tracheids and fiber-tracheids with very thin to thick walls. The vessel elements are medium-sized and have sloping end walls. Intervascular pitting is very small to medium-sized, opposite (some) and alternate; spiral thickenings occur in

the vessels of the members of one tribe (Coryleae). Vascular rays are homogeneous I or heterogeneous IIB; they are mostly 1 to 4 cells wide, and up to 80, mostly 60 cells high. Aggregate rays are common among the species. Crystals may occur in the ray cells. Wood parenchyma is diffuse, metatracheal and terminal, and scanty to relatively abundant in amount. Pith flecks are common.

2. Betula is characterized by the presence of very small, alternate intervascular pits with confluent apertures, and scalariform perforation plates with numerous narrow bars, but with a tendency to reduce the number of bars. Both tracheids and fiber-tracheids occur. Aggregate rays are generally lacking, except in the sub-section Nanae. Parenchyma is diffuse, terminal and metatracheal. Rays are homogeneous I.

3. In Alnus the intervascular pitting is small, opposite and alternate; the perforation plates are scalariform with numerous, narrow bars. Tracheids and fiber-tracheids occur. The vascular rays are homogeneous I, and there is a tendency toward elimination of multiseriate rays. Aggregate rays are common. The parenchyma is mostly diffuse and metatracheal.

4. In Ostryopsis and Corylus, which are indistinguishable anatomically, the intervascular pitting is medium-sized and alternate. Spiral thickenings occur in the vessels. Fibrous elements are tracheids exclusively. Vascular rays are heterogeneous IIB, and aggregate rays are present. Parenchyma is diffuse, metatracheal, and terminal. Perforation plates are scalariform, with intermediate to few, wide bars.

5. Carpinus differs from the two preceding genera in a marked tendency toward reduction in the number of bars in the perforation plates. Some species have plates with few, wide bars, while others have simple perforations with vestiges of bars. Spiral thickenings in the vessels, aggregate rays, and alternate intervascular pitting are also present. The vascular rays are homogeneous I. Parenchyma is diffuse, terminal and metatracheal.

6. In Ostrya there are no scalariform perforation plates, but simple perforations only, though vestiges of the bars may occur. Aggregate rays are also lacking. Otherwise this genus is similar in most respects to Carpinus.

7. The trends of specialization as indicated by wood anatomy are, in the Betuleae, from Alnus (scalariform perforation plates with numerous, narrow bars; opposite and alternate intervascular pitting) to Betula (reduction in the number of bars and widening of the bars in the perforation plates; exclusively alternate intervascular pitting); thence in the tribe Coryleae, to Corylus and Ostryopsis (spiral thickenings in the vessels, fiber-tracheids exclusively, reduced number of wide bars in the scalariform perforation plates, heterogeneous rays), to Carpinus (marked tendency toward simple perforations, homogeneous rays) and to the most advanced genus, Ostrya (simple perforations, homogeneous rays etc.).

8. The family Betulaceae is taxonomically divisible into two tribes, the Betuleae and the Coryleae. In the tribe Betuleae the perforation plates are exclusively scalariform, the intervascular pitting is opposite to alternate, there are tracheids as well as fiber-tracheids, there are no spiral thickenings in the vessels, and the vascular rays are homogeneous. In the tribe Coryleae there is a marked tendency toward simple perforation plates, intervascular pitting is exclusively alternate, the fibrous elements are exclusively fiber-tracheids, there are spiral thickenings in the vessels, and the vascular rays are heterogeneous or homogeneous. These two tribes have been raised to family rank by some taxonomists. A final decision in this must await further research, especially taxonomic studies.

Anatomical evidence indicates that the Betulaceae are not primitive, but are moderately advanced. The occurrence of homogeneous rays, alternate intervascluar pitting, spiral thickenings in the vessels and simple perforations in some species are indications of specialization. Certain unspecialized characters, such as very numerous, very small, angular, thin-walled vessels, scalariform vessel elements in some

species, and medium-sized vessel elements indicates that the specialization of the family is only moderately advanced.

Anatomical evidence precludes the Casuarinaceae as an ancestral type for the Betulaceae, since the Casuarinaceae are anatomically more highly specialized. The Hamamelidaceae, an anatomically unspecialized family, are suggested as an ancestral group.

Evidence from other fields of botany is introduced to support a moderately advanced position for the Betulaceae and the possible origin from hamamelidaceous ancestors.

Gametophyte development is reviewed, and the similarities to the Casuarinaceae and Hamamelidaceae are indicated. Chalazogamic fertilization and multiple embryo sacs are characters found in the Casuarinaceae and Betulaceae, and the occurrence of numerous megaspores is shared by all three families; it is suggested that the similarities of the Betulaceae and Casuarinaceae do not indicate a direct relationship between them, but suggest a derivation from common ancestor, such as some pre-hamamelidaceous stock.

Floral and inflorescence anatomy and floral morphology in the Betulaceae indicate modifications from a former hexamerous floral plan, involving reduction in number of parts and entire florets, compression within the ament, fusion of parts, and shortening of internodes within the ament.

Paleobotanical evidence shows that the Betuleae appeared in the geological record before Coryleae, supporting the anatomical evidence as to the relative primitiveness of the former tribe.

The nodes of the Betulaceae are of the primitive trilacunar type, as in the Hamamelidaceae. Pollen grains are acolpate, but there is little phylogenetic significance attached to this type. The haploid chromosome numbers are 8 and 14; the basic number is probably 7. Polyploid and hybridism have been reported among the species. The lenticles of the stem are of the primitive transverse type. In Sporne's table of

advancement indices, the Betulaceae are placed just below the midpoint, with an advancement index of 40.

The evidence from these other fields of investigation lends support to the conclusion that the Betulaceae are moderately advanced, and probably derived from some hamamelidaceous ancestor.

VITA

The author was born in Burlington, Vermont on December 30, 1918. He received his elementary and high school education in Massachusetts, graduating from Marshfield High School in 1936. Thereupon, he entered the University of Massachusetts, in Amherst, Massachusetts. As an undergraduate he majored in Pomology, and received the B.S. degree in 1940. In the fall of 1940 he entered the Graduate School of the University of Massachusetts, where he was given a teaching assistantship in botany which he held for two years. In 1942 he received the M.S. degree. In June of that year he entered the Army of the United States and served as personnel sergeant in the headquarters of a Quartermaster Batallion in this country and in the Southwest Pacific Theater. After his release from the Army in 1946 he was employed as analytical chemist by Schimmel and Company, New York, dealers in essential oils. In the spring of 1947 he was named to an assistantship in Botany at the University of Illinois, a position he held until he was appointed University Fellow in Botany in the fall of 1949. He is the author of "A morphoplastic interpretation of the amphivaasl bundle in Ranunculus" (Lloydia 10: 235-241, 1947), and "The genus *Anemone* in Illinois" (Trans. Ill. Acad. Sci. 41: 32-38, 1948). He is a member of the Botanical Society of America, American Society of Plant Taxonomists, American Association for the Advancement of Science, Illinois Academy of Science, and of the honorary societies of Phi Kappa Phi, Sigma Xi, and Phi Sigma.